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Short- and long-term consequences of early developmental conditions: a case study on wild and domesticated zebra finches

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Short title: Life-history strategies of wild and domestic birds

Abstract

Divergent selection pressures among populations can result not only in significant differentiation in morphology, physiology and behaviour, but also in how these traits are related to each other, thereby driving the processes of local adaptation and speciation. In the Australian zebra finch, we investigated whether domesticated stock, bred in captivity over tens of generations, differ in their response to a life-history manipulation, compared to birds taken directly from the wild. In a 'common aviary' experiment, we thereto experimentally manipulated the environmental conditions experienced by nestlings early in life by means of a brood size manipulation, and subsequently assessed its short- and long-term consequences on growth, ornamentation, immune function and reproduction. As expected, we found that early environmental conditions had a marked effect on both short- and long-term morphological and life history traits in all birds. However, although there were pronounced differences between wild and domesticated birds with respect to the absolute expression of many of these traits, which are indicative of the different selection pressures wild and domesticated birds were exposed to in the recent past, manipulated rearing conditions affected morphology and ornamentation of wild and domesticated finches in a very similar way. This suggests that despite significant differentiation between wild and domesticated birds, selection has not altered the relationships among traits. Thereby these results are reassuring as domesticated zebra finches are so widely used as a model species in the study of life-history evolution and sexual selection.

Keywords: brood size manipulation, common garden experiment, developmental stress, divergent selection, domestication, investment trade-off, life history strategy, maternal effects, sexual selection, *Taeniopygia guttata*

Introduction

Individuals face a trade-off of investing limited resources in somatic growth, body maintenance and / or reproduction (Stearns, 1992). The optimal solution to this allocation trade-off depends on the selection pressures imposed by the environment, such as food availability or habitat quality (Taborsky, 2006, Candolin *et al.*, 2007), predation risk (Reznick *et al.*, 2001), parasitism (Norris & Evans, 2000, Tschirren & Richner, 2006) or access to mating partners (Walling *et al.*, 2007).

Resource availability during early life stages represents a particularly strong selection pressure, with early developmental trajectories significantly shaping subsequent morphology, behaviour and physiology at adulthood (Lindström, 1999, Metcalfe & Monaghan, 2001). For example, numerous studies have demonstrated that a poor start in life results in reduced fecundity (Haywood & Perrins, 1992), longevity (Lummaa & Clutton-Brock, 2002), competitive ability (Royle *et al.*, 2005), and attractiveness (de Kogel & Prijs, 1996), although a recent study (Selesniemi *et al.*, 2008) did find positive effects of moderate caloric restriction *during adulthood* on female fecundity and offspring survival. Even if individuals reared under poor environmental conditions are able to compensate, or 'catch up', to some extent later in life when conditions become more favourable, full compensation is rare and potentially costly (Metcalfe & Monaghan, 2001). Therefore, manipulating the resource availability during growth provides an effective way of gaining insights into the trade-offs and investment priorities that operate on an individual and a population level.

The zebra finch, *Taeniopygia guttata*, is a classic avian model species, widely used in behavioural and evolutionary ecology research (Zann, 1996). Zebra finches are small, socially monogamous birds endemic to central Australia, which breed opportunistically following rainfall, when food resources are most favourable (Zann,

1996). Experiments manipulating brood size or food quality in domestic zebra finches held in captivity in Europe have found strong effects on traits such as growth, mortality, body size, ornamentation and attractiveness (de Kogel & Prijs, 1996, Birkhead *et al.*, 1999, Naguib *et al.*, 2008). These findings suggest that early nutritional conditions are an important determinant of lifetime fitness in this species. However, all of these previous studies have been conducted using domesticated birds, which have been bred in captivity for many generations. Even the study by Naguib *et al.* (2008) that used 'non-domesticated birds of wild Australian origin' was focused on a population of birds in Germany descended from 12 pairs taken from a captive population (of wild birds) in Australia in 1992 (Forstmeier *et al.*, 2007), and was thus exposed to lab selection for a number of generations.

The domestication process, and particularly the input from professional and amateur aviculturists, is likely to have subjected populations to selection for traits such as body size, body shape, ornamentation and broodiness in females (Sossinka, 1982, Zann, 1996, Rutstein et al. 2007). Thus, while selection on size and ornamentation may have been strong in these domesticated birds (see Zann, 1996, appendix in Forstmeier *et al.,* 2007), natural selection pressures (e.g. predation, unpredictable food availability, or parasitism), which are arguably the strongest selective pressures acting on populations in the wild (Zann, 1996), have been greatly relaxed. Indeed, there is good evidence that selection imposed by aviculturists and the captive environment has significantly shaped a number of morphological (Sossinka 1970; Zann, 1996) and behavioural traits (Rutstein *et al.*, 2007). For example, domesticated birds in Europe are approximately 50% heavier than their wild counterparts in Australia. In a cross-fostering experiment, in which offspring of wild-caught zebra finches were raised by domestic parents (and vice versa), we

could confirm that these differences have a genetic basis (Tschirren et al. unpublished data). However, we still know relatively little about whether these divergent selection pressures have affected the mean trait values only, or the (genetic) relationships amongst traits as well (Roff & Mousseau 2005). In other words, do wild and domesticated zebra finches have different life-history strategies, and do they resolve evolutionary trade-offs in different ways?

Here, we present a 'common aviary' experiment, in which we manipulated the environmental conditions experienced by offspring of domesticated and wild-caught birds early in life by means of a brood size manipulation experiment. This enabled us to examine both the short and long-term consequences of harsh and favourable early environmental conditions on investment in growth, sexual attractiveness, immune function and reproduction. Furthermore, the simultaneous manipulation of both domesticated and wild zebra finches allowed us to evaluate how vastly different selection pressures can shape resource allocation trade-offs, developmental trajectories and investment strategies within a species. It thereby provides us with important insights into the extent to which domesticated zebra finches can provide a suitable model organism for their wild conspecifics, and natural bird populations in general.

Methods

Birds and aviary set-up

We used wild adult zebra finches caught in November 2004 at East Mandelman on the Fowlers Gap Arid Zone Research Station in Western New South Wales, Australia (31°05'S, 142°43'E), and domesticated adult birds obtained from three different finch

breeders around Sydney, New South Wales, Australia, for the experiments. The first breeding round was carried out in March 2006 using 84 wild-caught and 84 domestic birds that had been held in aviaries under identical conditions. Fourteen birds (7 females / 7 males) were released in each of 12 aviaries, each measuring 4 x 2.3 x 2.4 m, with wild and domestic birds being kept in separate aviaries, visually isolated from one another. The aviaries were alternated, with wild birds in the first aviary, domestic birds in the second aviary, and so on. Each aviary contained 12 nest boxes, nest material, and *ad libitum* finch mix (Golden Cob® Premium Finch Mix, Masterfoods), water and cuttlebone. Spinach was provided once a week. A second breeding round was carried out in October 2006 with a further 60 domestic and 60 wild-caught birds, using an identical aviary set-up.

Manipulation of early growth conditions

Nest boxes were checked twice weekly for eggs, which were marked and measured (length and breadth) to the nearest 0.1 mm with digital callipers. From the start of hatching, next boxes were checked three times a week. After hatching, nestlings were uniquely marked by removal of down feathers on the back and head. When chicks were 0 – 2 days old, they were partially (and randomly with respect to hatching order) cross-fostered between two or more nests, depending on the number of broods available with similarly aged nestlings, to create experimentally large (containing five chicks) or experimentally small broods (containing two chicks), which is within the natural range of brood sizes of this species (Zann, 1996; pers. obs.). Cross-fostering was performed within type only, i.e. wild chicks were only exchanged with wild chicks, and domestic chicks with domestic chicks.

During the first breeding round we created 63 experimental broods (15 large

149 domestic, 15 small domestic, 19 large wild and 14 small wild broods). In round two
150 we created 28 experimental broods (5 large domestic, 6 small domestic, 7 large wild
151 and 10 small wild broods). There was no significant difference in original clutch size
152 among treatment groups ($F_{1, 89} = 0.55$, $P = 0.46$), and there was no difference in the
153 mass at cross-fostering of chicks that were allocated to large or small broods
154 respectively ($F_{1, 288} = 2.02$, $P = 0.16$).
155
156 *Nestling measures*
157 Nestlings were weighed at cross-fostering on an electronic balance to the nearest 0.1
158 g, and this was continued every 2 – 3 days until they were big enough to be given a
159 plastic, numbered leg ring for identification. At ringing (approx. day 12), we also
160 measured tarsus length to the nearest 0.1 mm with digital callipers, and removed a
161 tail feather. Using digital callipers, we measured the proportion of the fully developed
162 feather and the part that was still covered with a waxy sheath to the nearest 0.1 mm.
163 Chicks that develop faster have a relatively smaller waxy sheath. We thus used (1 –
164 length waxy sheath / total tail feather length) as a proxy of developmental rate. This
165 ratio was subsequently arcsine square-root transformed for the statistical analyses
166 (Sokal & Rohlf, 1981).
167 Offspring were kept in their rearing aviaries until sexual maturity (at 90 days old), at
168 which time they were moved to single-sex cages, measuring 75 x 40 x 30 cm. They
169 were provided with *ad libitum* finch mix, cuttlebone and water, and additional spinach
170 was given once a week. The animal house containing the single-sex cages was lit
171 with full-spectrum lights (light regime: 14 h light : 10 h dark), and maintained at a
172 temperature between 20 – 23ºC.
173

174 *Adult morphology and immune response*

175 At sexual maturity, we measured body mass to the nearest 0.5 g using a Pesola
176 balance. Metatarsus, wing, bill and tail length were measured to the nearest 0.1 mm
177 using digital callipers. We performed a Principle Component analysis with these four
178 measures of body size. Body size PC1 explained 59.5% of the variation
179 (Eigenvector: metatarsus: 0.44, bill: 0.49, wing: 0.56, tail: 0.50).
180 The birds' immunocompetence was assessed by the PHA skin test (Smits *et al.*,
181 1999, Tella *et al.*, 2002, Martin *et al.*, 2006). We injected birds subcutaneously with
182 0.1 mg of PHA-P (SIGMA Chemicals) dissolved in 0.02 ml of sterile phosphate-
183 buffered saline (PBS) in the centre of the left wing-web (Tschirren *et al.*, 2007). The
184 thickness of the wing-web at the injection site was measured with a micrometer
185 (Mitotuyo, Switzerland) to the nearest 0.01 mm before and 24 h (± 0.5 h) after
186 injection, and the difference in swelling was used as a measure of
187 immunocompetence (Smits *et al.*, 1999).
188
189 *Adult bill coloration*
190 We made objective measures of bill colour, which is believed to be a sexually
191 selected trait in this species (Burley & Coopersmith, 1987, Zann, 1996, Blount *et al.*,
192 2003b, Birkhead *et al.*, 2006), using a USB2000 spectrometer (Ocean Optics,
193 Dunedin, USA) and fibre-optic reflectance probe coupled to a xenon light source
194 (Ocean Optics PX-2). To measure the reflectance spectra we held the optic fibre at
195 90° to the bill. A white reference (WS-2, Avantes) was used to standardize the
196 reflectance of each measurement. Three measures of bill colour were taken, and
197 averaged before processing the reflectance spectra using the freeware program
198 SPEC (Hadfield, 2005) following the methodology presented by Hadfield *et al.*

(2006). This method is superior to segment-based estimates of colour variation such as calculated 'chroma', 'brightness' and 'hue' because it uses all of the reflectance data and makes no prior assumptions about what might be important. Most importantly it accounts for the passerine visual system, calculating the amount of light reflected across the visual spectrum allowing for the spectral sensitivity of the four visual cones (Hart *et al.,* 2000), producing four quantal cone catches (very short, short, medium and long wavelength) (Vorobyev *et al.,* 1998). These four quantal catches were transformed into three independent log contrasts using the long wavelength catch as a denominator (Endler & Mielke, 2005). These three log-contrasts (c_{1-3}) were used in a Principle Component Analysis: PC1 explained 90.8% of the colour variation (Eigenvector, c_1: 0.59, c_2: 0.57, c_3: 0.58), PC2 explained 6.3% of the variation (Eigenvector, c_1: -0.32, c_2: 0.82, c_3: -0.48), and PC3 explained 2.9% of the variation (Eigenvector, c_1: -0.75, c_2: 0.09, c_3: 0.66). High colour PC1 scores thus indicate relatively more light being reflected at very short, short and medium wavelengths. Higher colour PC2 scores indicate more reflection at short, but less reflection at very short and medium wavelengths, and high colour PC3 scores indicate more reflection at medium wavelengths, but less reflection at very short wavelengths.

Adult song rate

Beside bill colour, song rate has previously been found to be an indicator of male attractiveness in zebra finches (Houtman, 1992, Collins *et al.*, 1994, Forstmeier & Birkhead, 2004, Spencer *et al.*, 2005, Rutstein *et al.*, 2007). We measured male song rate using the methodology described by Birkhead *et al.* (1998) and Rutstein *et al.* (2007) and recorded the total amount of song (in seconds) that a male produced

224 during a five-minute period when placed in a cage with a female. For each male, this
225 was repeated with five different females on separate days, and the mean of the five
226 trials was calculated. Song rate was repeatable within males over the five trials (R =
227 0.69, SE = 0.04, Lessells & Boag, 1987).
228
229 *Reproductive success*
230 To assess the long-term consequences of early environmental conditions on the
231 birds' reproductive success, adult offspring from the first breeding round (N = 36
232 large domestic, 21 small domestic, 41 large wild, 19 small wild birds) were released
233 into 12 aviaries (again, wild and domestic birds were kept separately) to mate and
234 breed freely. We recorded laying date, clutch size and egg volume of these broods
235 as described above.
236
237 *Statistical Analyses*
238 We used mixed-model ANOVAs and ANCOVAs for the analysis of treatment and
239 type effects and logistic regressions for survival analyses using JMP V5 (Sall &
240 Lehmann, 1996).
241 Treatment (experimentally small or large brood size), type (wild or domestic) and
242 their interaction were entered as fixed factors, and breeding round, nest of rearing
243 and nest of origin were entered as random effects into the model. Nestling age was
244 included as a covariate to control for age-related variation in nestling measures.
245 Analysis followed a backwards-stepwise procedure whereby all biologically relevant
246 variables and interactions were initially included and non-significant interactions were
247 sequentially removed from the model. We used least-squares means contrasts for
248 the analysis of differences between birds raised in experimentally small or large

broods within a given type. All tests were two-tailed with a significance level of P d 0.05. Residuals of the models were tested for normality using Shapiro-Wilk tests and homoscedasticity using Bartlett tests to ensure that the assumptions for parametric testing were fulfilled. Sample sizes differ among analyses because of mortality or missing measurements.

Results

Clutch and egg size

Wild-caught and domestic females laid similar sized clutches (mean ± 1 SD: domestic: 5.08 ± 1.2 eggs, N = 49 clutches, wild: 4.78 ± 1.2 eggs, N = 60 clutches, $F_{1, 107}$ = 1.65, P = 0.20). However, domestic females laid significantly larger eggs both in absolute terms (mean egg volume ± 1 SD: domestic: 1031.1 ± 88.3 mm^3, wild: 938.2 ± 90.5 mm^3, $F_{1,107}$ = 29.04, P < 0.001, and when including female mass as a covariate: type: $F_{1,106}$ = 8.19, P = 0.005, female mass: $F_{1,106}$ = 14.19, P < 0.001).

Nestling growth and development

At cross-fostering, offspring of domesticated birds (N = 128 nestlings) were heavier than offspring of wild-caught birds (N = 162 nestlings) ($F_{1,136}$ = 8.92, P = 0.003), and this difference in body mass between types became stronger during the nestling period (body mass at ringing: $F_{1,137}$ = 22.31, P < 0.001; tarsus length: $F_{1,134}$ = 2.50, P = 0.12).

Within three days of the brood size manipulation, nestlings were significantly heavier in experimentally small broods (N = 90 nestlings) than in experimentally large broods (N = 223 nestlings) ($F_{1,155}$ = 15.99, P < 0.001), and this difference remained

274 significant through to ringing (body mass: $F_{1,137} = 46.69$, $P < 0.001$; tarsus length:
275 $F_{1,134} = 12.55$, $P < 0.001$). However, the growth of domestic and wild birds was
276 affected in a similar way by the brood size manipulation as demonstrated by the non-
277 significant interaction term (treatment x type; body mass at ringing: $F_{1,136} = 1.80$, $P =$
278 0.18; tarsus length at ringing: $F_{1,133} = 0.15$ $P = 0.70$; $N = 87$ large domestic, 41 small
279 domestic, 121 large wild, 44 small wild nestlings).
280 Surprisingly, nestlings from large broods developed faster, as measured by tail
281 feather development, than nestlings from small broods ($F_{1,99} = 14.08$, $P < 0.001$, Fig.
282 1). There was no significant difference in the developmental rate of wild and domestic
283 nestlings ($F_{1,99} = 0.07$, $P = 0.80$), and no significant interaction effect between type
284 and treatment ($F_{1,98} = 1.67$, $P = 0.20$; $N = 76$ large domestic, 37 small domestic, 96
285 large wild, 42 small wild nestlings).
286 26 of 319 nestlings died between hatching and ringing. Nestling mortality was
287 not significantly different between wild and domestic birds (Wald $\chi^2_1 = 1.08$, $P =$
288 0.30), or between nestlings from large and small broods (Wald $\chi^2_1 = 1.10$, $P = 0.29$;
289 interaction: Wald $\chi^2_1 = 2.92$, $P = 0.09$).
290 Survival to adulthood was higher for domestic birds raised in small broods
291 (4.9% mortality) compared with domestic birds raised in large broods (24.0%
292 mortality). This survival benefit of favourable early conditions was absent in wild
293 offspring (large broods: 25.6% mortality, small broods: 22.9% mortality; interaction
294 treatment x type: Wald $\chi^2_1 = 3.79$, $P = 0.052$).
295
296 *Adult mass and size*
297 At adulthood, offspring of domesticated birds were significantly heavier ($F_{1,97} = 90.48$,
298 $P < 0.001$) and larger (body size PC1: $F_{1,97} = 78.55$, $P < 0.001$) than offspring of wild-

caught birds (Fig. 2a, b). Furthermore, birds originating from experimentally small broods were heavier ($F_{1,97} = 13.15$, $P < 0.001$) and larger ($F_{1,97} = 11.18$, $P = 0.001$) as adults than offspring from experimentally large broods (Fig. 2a, b). Again, there was no significant interaction between type and treatment on adult body mass ($F_{1,96} = 0.05$, $P = 0.82$) or body size ($F_{1,96} = 0.01$, $P = 0.94$; $N = 76$ large domestic, 40 small domestic, 96 large wild, 37 small wild birds).

Adult immune response

Domestic birds had a significantly stronger PHA response than wild birds ($F_{1,87} = 28.49$, $P < 0.001$), and there was a significant interaction effect between type and treatment ($F_{1,87} = 5.27$, $P = 0.024$, Fig. 3). Domestic birds from large broods ($N = 75$) mounted a stronger immune response than domestic birds from small broods ($N = 39$; contrast: $F_{1,87} = 11.53$, $P = 0.001$), but there was no difference in immune response between wild birds reared in large ($N = 87$) and small broods ($N = 37$; contrast: $F_{1,87} = 0.03$, $P = 0.86$), respectively (Fig. 3).

There was a positive association between a bird's body mass and PHA response ($F_{1, 86} = 3.97$, $P = 0.050$). However, the effects of treatment ($F_{1, 86} = 8.07$, $P = 0.006$), type ($F_{1, 86} = 7.86$, $P = 0.030$) and their interaction ($F_{1, 86} = 4.86$, $P = 0.030$) remained significant when including body mass as a covariate into the analysis of PHA response. It shows that the stronger immune response of domestic birds cannot simply be explained by their bigger mass.

Adult bill colour

Bill colour was not significantly different between wild and domestic birds (PC1: $F_{1, 98} = 0.02$, $P = 0.88$, PC2: $F_{1, 98} = 1.80$, $P = 0.18$, PC3: $F_{1, 98} = 1.00$, $P = 0.32$), nor was it

influenced by the brood size manipulation (PC1: $F_{1, 98} = 2.96$, $P = 0.09$, PC2: $F_{1, 98} = 2.09$, $P = 0.15$, PC3: $F_{1, 98} = 0.91$, $P = 0.34$). None of the interactions between type and treatment on bill colour were statistically significant (all $P > 0.31$; $N = 76$ large domestic, 40 small domestic, 97 large wild, 37 small wild birds).

Adult song rate

Contrary to our expectations, mature males that had grown up in experimentally enlarged broods sang significantly more than males from small broods ($F_{1,18} = 5.49$, $P = 0.031$, Fig. 4). There was no overall difference in song rate between domestic and wild males ($F_{1,18} = 0.85$, $P = 0.37$), and we found no significant interaction effect between type and treatment on song rate ($F_{1,18} = 0.00$, $P = 0.96$; N = 17 large domestic, 9 small domestic, 10 large wild, 9 small wild males).

Reproductive success

To assess the long-term consequences of early conditions, we measured the reproductive success of adult birds originating from experimentally small and large broods. Laying date was not significantly influenced by female treatment ($F_{1,25} = 0.34$, $P = 0.56$), or male treatment ($F_{1,25} = 0.14$, $P = 0.71$), and none of the interactions between treatment and type were statistically significant (all $P > 0.11$). Similarly, there was no significant effect of female treatment or male treatment on clutch size (female treatment: $F_{1,25} = 0.47$, $P = 0.50$; male treatment: $F_{1,25} = 0.00$, $P = 0.97$) or mean egg size (female treatment: $F_{1,25} = 1.81$, $P = 0.19$; male treatment: $F_{1,25} = 0.10$, $P = 0.76$; all interactions $P > 0.15$).

Discussion

We investigated how the different selection pressures, to which wild and domesticated zebra finches have been exposed over recent generations (Sossinka, 1982, Zann, 1996), have shaped resource allocation trade-offs, developmental trajectories and investment strategies when facing favourable or harsh conditions early in life. We found strong effects of manipulated brood size on body size and body mass in offspring of both wild-caught and domesticated finches from an early age. These differences remained significant through to adulthood, with individuals from experimentally large broods being significantly smaller and lighter, even though all birds were kept under identical conditions after fledging and had access to *ad libitum* food. This demonstrates that even if conditions become more favourable later in life, individuals cannot fully compensate for a poor start in life (Metcalfe & Monaghan, 2001).

The effects of manipulated brood size on developmental rate were surprising at first sight; even though nestlings raised in experimentally large broods were significantly smaller and lighter, their developmental rate, as measured by tail feather development, was significantly higher. Previous studies have shown that rapid development can lead to increased free radical production (Mangel & Munch, 2005, Johnsson & Bohlin, 2006, Alonso-Alvarez *et al.*, 2007, de Block & Stoks, 2008), and is therefore costly. Furthermore, zebra finch nestlings raised under poor conditions have a reduced antioxidant assimilation capacity (Blount *et al.*, 2003a), which might further increase the costs of accelerated development for poor quality young. It thus seems counter intuitive that poor quality nestlings would develop faster than good quality chicks. However, Naguib *et al.* (2004) have previously found that zebra finch

372 nestlings raised in enlarged broods have higher circulating testosterone levels, which
373 might be the proximate cause of the accelerated development in this group.
374 Ultimately, fast development, and thus early fledging, might be an optimal strategy for
375 nestlings facing harsh rearing conditions, as they might thereby most efficiently
376 increase their short-term access to food, and thus their long-term prospects.
377 Alternatively, fast development and early fledging might be a strategy to reduce the
378 risk of predation when growing up in a large, noisy brood (Haskell, 1994, Leech &
379 Leonard, 1997).

380 In general, offspring of domesticated and wild-caught birds responded in a
381 very similar way to poor and favourable early conditions. We found no significant
382 interaction effect between type and treatment on nestling body mass, nestling body
383 size, or developmental rate. The latter is especially surprising as investment in traits
384 geared towards rapid development and early reproduction might be under particularly
385 strong selection in wild zebra finches. This is because short and unpredictable
386 breeding seasons and high annual mortality rates, combined with high nest predation
387 rates impose high pressure to breed early in life in this species (Zann, 1996). Captive
388 birds, on the other hand, have access to *ad libitum* food and water, and are therefore
389 able to breed all year round (Zann, 1996). Consequently, selection on developmental
390 rate might be mitigated in these birds. However, in our study we found no indication
391 that offspring of wild birds prioritised development in general, and when facing harsh
392 environmental conditions in particular.

393 Similarly, we found little evidence that birds from wild and domestic
394 background had different resource allocation strategies or investment priorities in
395 traits measured at adulthood. Although offspring of domestic birds were generally
396 bigger and heavier as adults compared to offspring of wild-caught birds, we found no

significant differences in bill colour or song rate between the two types. Moreover, no significant interaction effect between type and treatment was observed on adult body mass, body size, song rate or bill colour. Again, these results indicate that domesticated birds do not prioritise their investment in ornamentation in general, and when facing poor conditions early in life in particular. This suggests that, in spite of vastly divergent selection pressures these populations have experienced in the past, the allocation strategies and general relationships between traits have not been significantly altered by domestication.

Nevertheless, we did find significant interaction effects between type and treatment on immune response and mortality. Domestic birds raised in small broods survived significantly better to adulthood compared with domestic birds raised in experimentally large broods (see also de Kogel & Prijs, 1996). This survival benefit of favourable early conditions was absent in wild offspring. Furthermore, immune response of domestic birds raised in experimentally large broods was significantly stronger than in domestic birds raised in small broods, whereas wild birds had low levels of immune response as adults, irrespective of the conditions experienced early in life. A direct trade-off between investment in immune defence and growth has previously been demonstrated in passerines (Soler *et al.*, 2003, Brommer, 2004, Tschirren & Richner, 2006), and domestic nestlings raised in large nests might thus have preferentially invested in immune defence on the expense of growth (see above). Such an investment strategy could be beneficial because the transmission of parasites or pathogens might be increased in crowded nests.

Interestingly, our results contrast those of comparable studies performed in European captive zebra finch populations, where nestlings raised under poor condition showed generally a lower PHA response (Birkhead *et al.*, 1999, Naguib *et*

al., 2004). This discrepancy might be due to the fact that we measured immune response at adulthood rather than during the nestling stage, as had been the case in most previous studies. Because of the higher mortality rates of domestic birds raised in large nests, selection against poor quality chicks might thus have biased the results for adult immune response. Alternatively, domestic birds from large broods might have overcompensated their low nestling immunocompetence (Birkhead *et al.*, 1999, Naguib *et al.*, 2004) as adults, leading to the discrepancy between previous work and our findings here. Also, aviary birds in Europe and Australia, respectively, might be exposed to different parasites or pathogens, which may have also contributed to these conflicting patterns of immune defence in different studies.

Both bill colour and / or song rate, have previously been found to be sexually-selected traits in zebra finches (Burley & Coopersmith, 1987, Collins *et al.*, 1994, de Kogel & Prijs, 1996, Birkhead *et al.*, 1998, Birkhead *et al.*, 1999, Rutstein *et al.*, 2007). However, unlike de Kogel & Prijs (1996), we found no indication that poor rearing conditions negatively affected bill colour at adulthood, despite the fact that our measure of bill colour through reflectance spectrometry was more objective and comprehensive than previous methods based on scoring bill colour against colour standards by eye. Furthermore, we found that adult males reared in experimentally large broods sang for a longer, rather than a shorter, period when facing a potential mating partner. This latter result is especially surprising given that reduced song rates in males reared in experimentally enlarged broods have previously been observed in a Dutch (de Kogel & Prijs, 1996) and a German (Naguib *et al.*, 2008) population, whereas no long-term effects of early conditions on adult song were found in other studies (Birkhead *et al.*, 1998, Birkhead *et al.*, 1999, Gil *et al.*, 2006). Whatever the reason for these different long-term effects of early rearing conditions

447 on adult song, it is unlikely to be due to different degrees of domestication among
448 study populations (Forstmeier *et al.*, 2007), as we found increased song rates in
449 males from experimentally large broods of both types, i.e. in offspring of wild-caught
450 and domesticated birds. Furthermore, it is unlikely that selection against poor quality
451 chicks in experimentally large broods has caused this effect, because in wild birds
452 mortality did not differ among small and large broods, but nevertheless males from
453 large broods sang longer.

454 A recent study in zebra finches has found long-term, transgenerational effects
455 of manipulated growth conditions of the mother (i.e. a brood size manipulation
456 experiment as in our study) on offspring body size, as well as on the hatching and
457 fledging success of their brood (Naguib & Gil, 2005, Naguib *et al.*, 2006). These
458 findings link early developmental stress in females with the phenotype of the next
459 generation via maternal effects, potentially via altered maternal yolk hormone
460 deposition (Gil *et al.*, 2004). Here, we found no significant long-term consequences of
461 poor growth condition on reproductive success in either wild or domestic birds.
462 Neither egg size, clutch size nor the start of reproduction were significantly influenced
463 by manipulated growth conditions of the mother or the father. However, our sample
464 size was small and the power to detect such differences and especially interaction
465 effects between type and parental treatment was therefore low. Furthermore,
466 conditions in the aviaries might have been too benign to produce a significant
467 difference in reproductive success between birds raised under favourable or harsh
468 conditions.

469 In conclusion, our brood size manipulation experiment was effective in
470 producing short- and long-term differences in a number of important morphological,
471 immunological and ornamental traits. Furthermore, we found large differences in the

absolute expression of traits among offspring of wild-caught and domesticated birds reared under identical conditions (see also Forstmeier *et al.*, 2007). However, we found little evidence that the different selective regimes, to which wild and domestic zebra finches have been exposed to over the past generations, have altered the relationships among traits, and thereby developmental trajectories or investment strategies, and the resolution of resource allocation trade-offs in general, when facing favourable or harsh conditions early in life. This is a reassuring finding in the light of the widespread use of domestic zebra finches as a model species in behavioural ecology research, and suggests that adaptive explanations may be legitimate when referring to studies of captive, and domesticated birds.

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633 **Figure legends**

634 **Fig. 1** Feather development of domestic and wild nestlings raised in experimentally
635 large or small broods. Feather development was measured as 1 – length of feather
636 wax sheath / total tail feather length and is a proxy for developmental rate. Different
637 letters above bars indicate significant differences; error bars indicate SE.

638

639 **Fig. 2** a) Adult body mass and b) adult body size of domestic and wild birds raised in
640 experimentally large or small broods. Body size PC1 explained 59.5% of variation in
641 metatarsus, bill, wing and tail length. Different letters above bars indicate significant
642 differences; error bars indicate SE.

643

644 **Fig. 3** Adult immune response of domestic and wild birds raised in experimentally
645 large or small broods. Immune response was measured with the PHA skin test.
646 Different letters above bars indicate significant differences; error bars indicate SE.

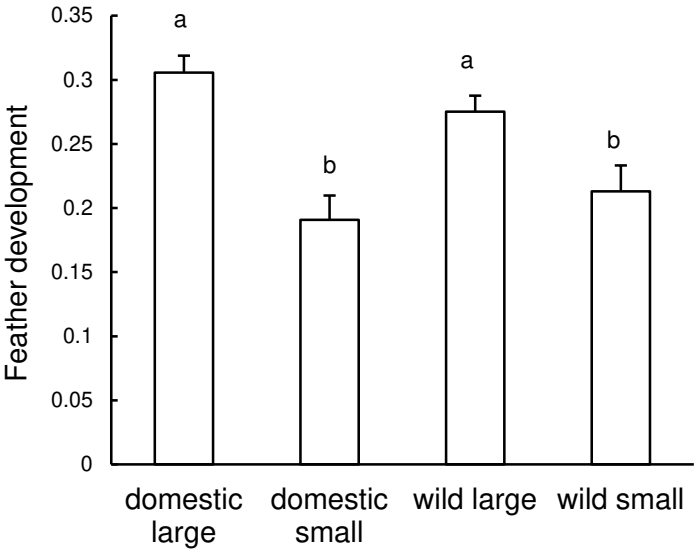
647

648 **Fig. 4** Adult song rate of domestic and wild males raised in experimentally large or
649 small broods during a 5 minute-exposure to a female. Different letters above bars
650 indicate significant differences; error bars indicate SE.

651

652 Fig. 1

653



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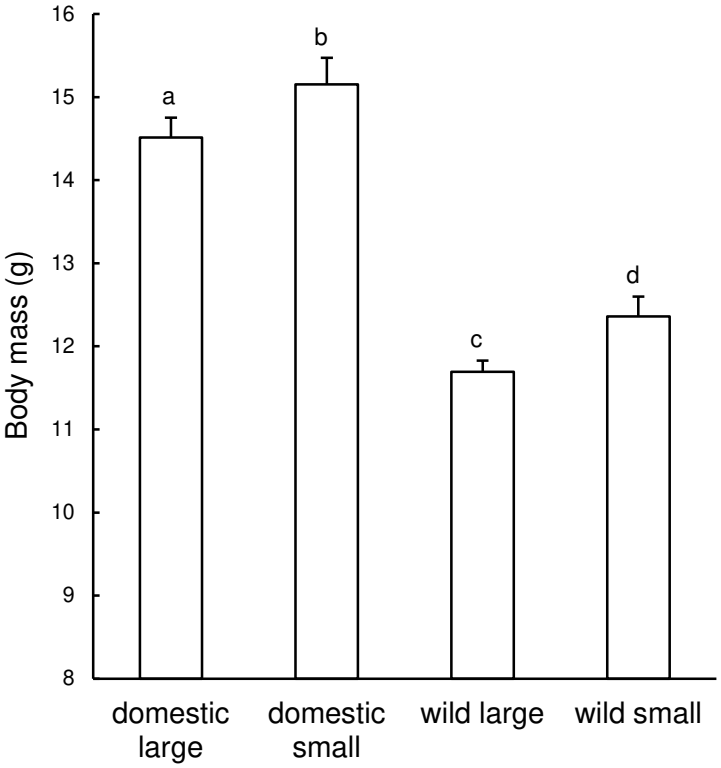
655

656 Fig. 2a



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660 Fig. 2b

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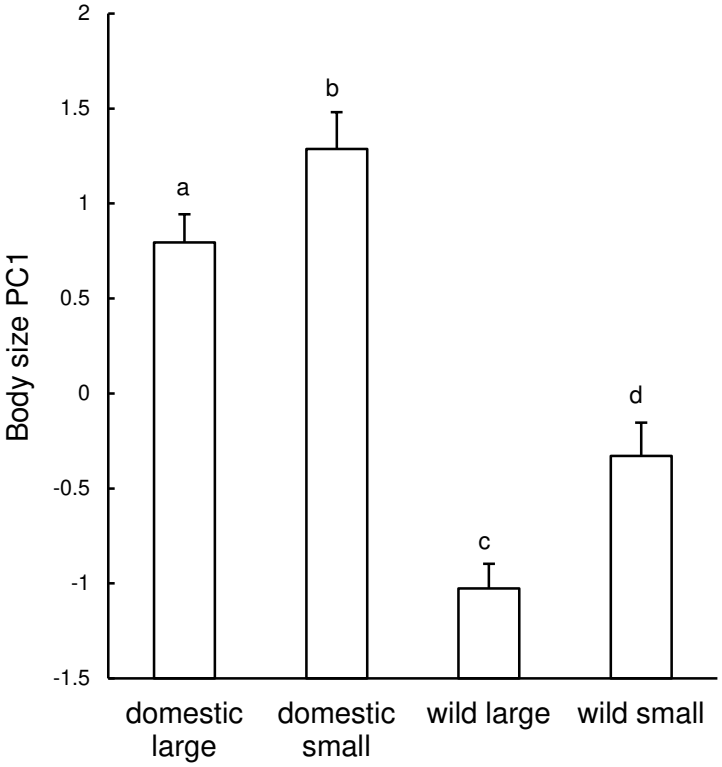

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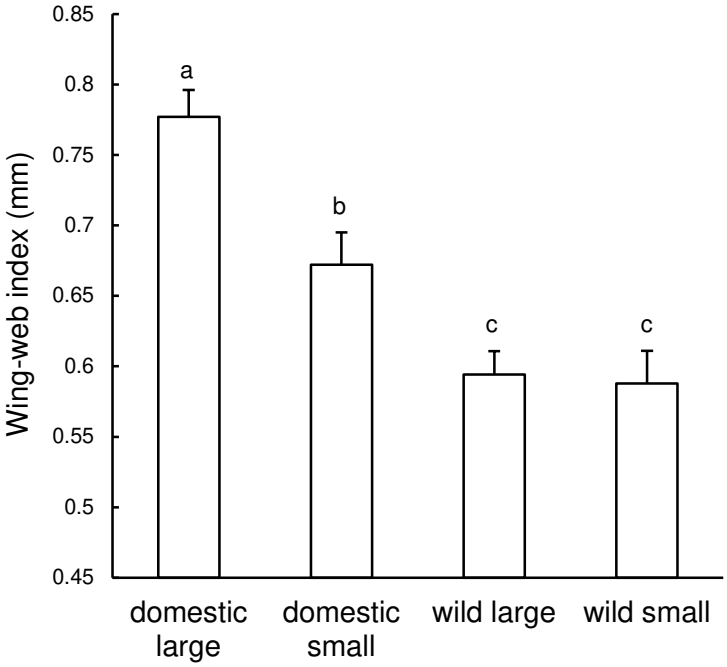
664 Fig. 3



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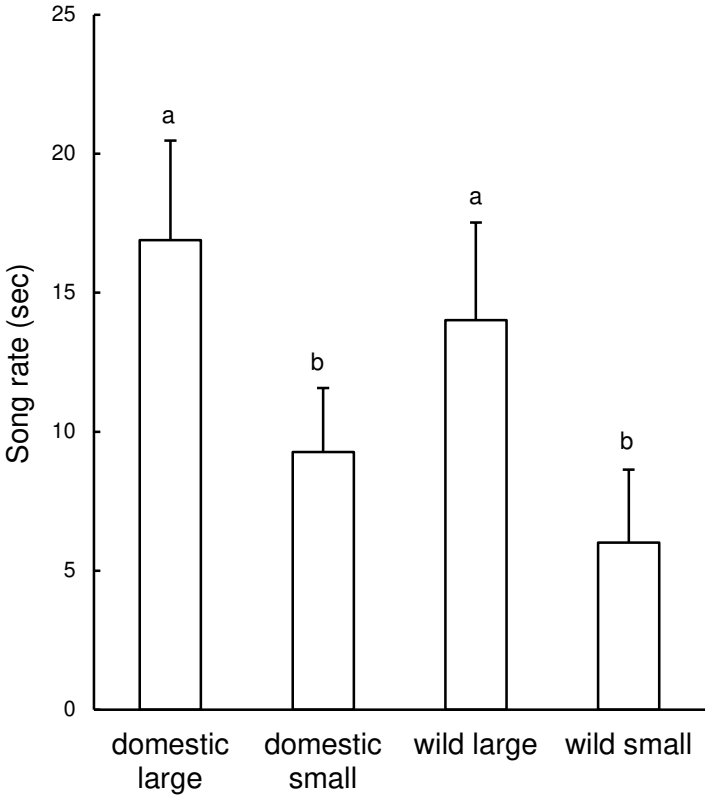
669 Fig. 4


25
20
15
10
5
0
Song rate (sec)
a
b
a
b
domestic large
domestic small
wild large
wild small

670